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Research Article

Phenological gap in fruiting period and dispersal of seeds from alien fleshy-fruited plants by medium-sized carnivores in temperate forests of Central Europe

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Abstract

Some biological differences between native and alien plants are relevant to their dispersal mechanisms. One of them is the fruiting period: it is shifted in time, peaking later than in natives. Here we report the case study showing the temporal distance in fruiting phenology between native and alien plants and their seed dispersal via carnivorous mammals. From 2009 to 2011, scats of badgers *Meles meles*, foxes *Vulpes vulpes*, martens *Martes* spp. (*M. martes* and *M. foina*) and possibly also raccoon dogs *Nyctereutes procyonoides* (N = 820) were collected along transects totaling 30.4 km in length each month from June to November. We analyzed the frequency of occurrence of seeds (FO%) and the seed load in sampled scats; 61.7% of the sampled feces contained seeds of 18 fleshy-fruited native and alien plant taxa, and the most abundant seeds were from species with multi-seeded fruits such as *Vaccinium myrtillus* (94.6%), *Rubus* sp. (2.0%), and drupes of *Prunus serotina* (1.0%). The structure of dominance was characterized by seeds of *Vaccinium myrtillus* (15.0%), *Pyrus* sp. (14.8%) and *Prunus serotina* (13.0%) with aliens reaching high frequency of occurrence (FO%). The shares of seed FO% in the samples differed between alien and native plants. For seed load there were also significant interactions between the status of the seeds (alien or native) and the month of the vegetation period. Our data show the coincidence of two factors – the late fruiting period of alien plants and the decreasing availability of native fruits during the vegetation period. Such a set of factors may promote the dispersal of alien plant seeds by carnivorous mammals, which, unlike migrating birds, are constantly present in autumn. The limited availability of native fruits after their fruiting period, creating a phenological gap, makes alien plants the main source of fleshy-fruits at the end of vegetation period in forest ecosystems; this is expressed in high proportion of alien plants in seed FO%, and in significant interactions in the seed load in carnivore scats.

Key words: Alien plants, carnivores, fleshy fruits, fruiting phenology, seed dispersal

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Introduction

A principal consequence of intentional or unintentional introduction of plants in forests is that many alien species, with their different and variable impacts on the environment and habitat functioning (Pyšek et al. 2012; Lazzaro et al. 2020), have become permanent elements of the flora (Chmura 2004; Tokarska-Guzik 2005). According to the Global Naturalized Alien Flora database (GloNAF), in only the

temperate zone as many as 9036 alien species have been introduced (Pyšek et al. 2017), and the interactions between them and native plants and the natural environment are already so well established that the functioning of alien plant species is referred to as naturalization (Jiang et al. 2011; Danielewicz et al. 2016), manifested in natural regeneration in new communities (Dyderski and Jagodziński 2018) and successful entry into different vegetation patches (Kurek et al. 2015). One of the effects of their naturalization in forest ecosystems consists of close interactions between alien and native species of different taxa. Alien plant species disrupt the functioning of ecosystems at different levels of organization and may create self-specific communities that exert significant effects on neighboring individuals and whole assemblages, affecting, for example, soil physicochemical properties, understory vegetation (Stanek et al. 2020), microbial properties and enzymatic activity (Stanek et al. 2021). The introduction of alien species has impacts on trophic interactions and can alter the food preferences (Hull-Sanders et al. 2007; Chupp and Battaglia 2014; Wiatrowska et al. 2018) and assemblages of native phytophagous animals (Albrecht et al. 2014; Wiatrowska et al. 2023), and can become an integral part of the seed dispersal process, for example in jays and introduced oaks (Myczko et al. 2014; Wróbel et al. 2022). Finally, the fleshy fruits of alien plants are an important food source for native animals and are spread by them, mostly by birds (Gosper et al. 2005; Deckers et al. 2008) but also by carnivorous mammals (Fedriani et al. 2001; López-Bao and González-Varo 2011; Rost et al. 2012; Kurek 2015).

It is well known that numerous Central European carnivores are foraging opportunists (Erlinge 1986; Jędrzejewska and Jędrzejewski 2001; Tsuji et al. 2011; González-Varo et al. 2013). This is an effect of the periodic occurrence of some important prey species such as voles, amphibians, reptiles and invertebrates. In consequence, carnivores are faced with periodic shortages of animal food (Erlinge 1986). Fruits, which also occur seasonally, may act as a critical dietary supplement in temperate forests of Central Europe (Kwit et al. 2004). In general, fruits are nutritious, energy-rich and readily available, making them a valuable, important source of food for carnivores as well (Herrera 1989; Posłuszny et al. 2007). Exploitation of alternative food sources is typical of generalist carnivores (Martinoli et al. 2001), and frugivory is very common in carnivores in many regions of Europe (Herrera 1989; Virgós et al. 1999; Kurek 2015). There are many reports showing that fruits may reach quite high proportions in the diet of martens *Martes* spp. (Rzebik-Kowalska 1972; Goszczyński 1976, 1986; Tryjanowski 1997; Apáthy 1998; Baltrūnaitė 2001; Schaumann and Heinken 2002; Lanszki 2003; Posłuszny et al. 2007), European badgers *Meles meles* (Goszczyński et al. 2000), foxes *Vulpes vulpes* (Goszczyński 1986; Baltrūnaitė 2001; Diaz-Ruiz et al. 2011), brown bears *Ursus arctos* (Frąckowiak and Gula 1992; Vulla et al. 2009; García-Rodríguez et al. 2021) and also invasive raccoon dogs *Nyctereutes procyonoides* (Kauhala et al. 1998; Sidorovich et al. 2008; Kauhala and Kowalczyk 2011). But nutrition is not the only important dimension of fleshy fruit consumption by carnivores. This guild of animals also acts as a dispersal agent of the seeds of foraged fleshy fruits; there are a number of reports of endozoochory in carnivores, highlighting their role in seed dispersal and germination enhancement (Fedriani and Delibes 2009a, 2009b; Guitián and Munilla 2010).

Many fleshy-fruited plant genera in Central Europe, including *Rubus*, *Sorbus*, *Ribes*, *Prunus*, *Sambucus*, *Vaccinium*, *Frangula* and *Lonicera* (Rutkowski 2011)

potentially offer rich food resources and may be consumed by carnivores (Fedriani and Delibes 2009a, 2009b; Guitián and Munilla 2010; Kurek 2015). In recent centuries the number of established alien taxa producing fleshy fruits in Central European forests has significantly increased (Danielewicz and Wiatrowska 2012). Initially, some species used by humans mainly for food purposes (e.g. *Pyrus communis*) were introduced unintentionally (Volk et al. 2006). Later, with the development of planned forest management (19th century), many intentional introductions were aimed at boosting forest production through attempts to improve litter quality (Starfinger et al. 2003; Aerts et al. 2017), introduce species suitable for the reclamation of post-industrial sites (Horodecki and Jagodziński 2017) or augment the assortment of edible forest fruits (Danielewicz and Wiatrowska 2012).

The propagules of alien plants (including cultivars and hybrids) that bear fruits attractive to animals become subject to seed dispersal processes, and carnivores that eat fruits become seed vectors for both native (Gasson et al. 2009; Kurek and Holeksa 2015) and alien plants (Richardson et al. 2000; Traba et al. 2006). Among the alien plants, species that fruit later than native ones (*Prunus serotina*, *P. domestica*, *P. cerasifera*, *Pyrus* sp., *Malus domestica*, *Vitis* sp.) deserve special attention because phenological differences between exotic and native species may contribute to the success of the invaders (Wolkovich and Cleland 2011). Some authors have reported finding their seeds in the feces of carnivores (Goszczyński 1986; Jankowiak et al. 2008), but the dispersal of alien taxa by carnivores is insufficiently recognized in northern temperate Europe; most of the current relevant research is focused on more arid environments (Fedriani et al. 2001; López-Bao and González-Varo 2011; Rost et al. 2012) where the phenology and plant assemblages are quite different from those in northern temperate latitudes. For alien plants, the seed dispersal of which has generally been associated with birds (Gosper et al. 2005; Deckers et al. 2008), medium-sized carnivores are also known as complementary vectors of their seeds (Fedriani et al. 2001; López-Bao and González-Varo 2011; Rost et al. 2012; González-Varo et al. 2013; Pereira et al. 2019). New aspects of these relationships are still emerging (García-Rodríguez et al. 2021); seed dispersal of fleshy fruits by carnivorous mammals now seems to be a more complex mechanism than was expected, requiring broader analyses of the phenological shift of the fruiting period of native and alien plants and the associated effects on frugivory. This phenomenon has rarely been discussed in carnivores; it is a novel area of study of alien plant–animal interactions in temperate forest ecosystems, with special attention focused on the commonest European medium-sized carnivores. Our work is spurred by previous research showing that cultivated fleshy-fruited species formed a share of carnivore diets (Bermejo and Guitian 2000), with some seasonal differences in frugivory patterns (López-Bao and González-Varo 2011). That report states that the temporal discrepancy in fruiting phenology between native and alien plants benefits the seed dispersal of the latter by carnivores.

In view of the importance of fleshy fruits as a component of the diet of carnivorous mammals, we wanted to further explore their role as seed dispersers for fleshy-fruited alien plants in temperate forest ecosystems in Central Europe. Taking seed frequency and seed load in carnivore scats as measures of alien seed dispersal effectiveness, we assumed that the differences in fruiting phenology presented by most of the alien plant species versus native ones and the absence of native fruits after their fruiting period, creating a phenological gap, supports the effectiveness of seed dispersal of alien fleshy-fruited plants by medium-sized carnivores in forests.

Materials and methods

Study area

The research was carried out in Kampinos National Park (hereafter KNP), which covers ~385 km^2 northwest of Warsaw, Poland (52.26–52.40°N, 20.28–20.88°E), and ranges in elevation from 68 to 106 m above sea level, with 7.7 °C mean annual temperature, 550 mm annual precipitation and a vegetation period averaging 185 days. The forests (73% of KNP area) are dominated by oligotrophic and sandy habitats with Scots pine *Pinus sylvestris* (80.9% of forested area). At lower elevations are wet habitats with black alder *Alnus glutinosa* (13.6% of forested area). In small areas between the wet and dry habitats, oak-hornbeam forests developed on more fertile soils (Andrzejewski 2003). The average age of KNP tree stands is 67 years; stands older than 100 years cover 15% of the KNP area. Several settlements and small villages abandoned in the 1970s and 1980s, surrounded by orchards and fallows, are scattered across the forests.

Frangula alnus is the most common species of the group of fleshy-fruited plants that occur in the research area. Less abundant but also common are *Sorbus aucuparia*, *Juniperus communis* and the invasive species *Prunus serotina*. The remaining fleshy-fruited shrubs and trees, rare in the study area, are *Sambucus nigra*, *S. racemosa*, *Viburnum opulus*, *Prunus spinosa*, *Cornus sanguinea*, *Ribes nigrum*, *Ribes uva-crispa*, *Rhamnus cathartica*, *Berberis vulgaris*, *Rosa* sp., *Euonymus europaeus*, *E. verrucosus*, *Cerasus avium* and *Crataegus* sp. In the herb layer the most common fleshy-fruited species are *Vaccinium myrtillus*, *V. vitis-idaea*, *Convallaria majalis* and *Rubus* spp. Some cultivated trees (*Prunus domestica*, *P. cerasifera*, *Malus domestica*, *Pyrus* sp.) show a distribution associated with the abandoned settlements. *Pyrus* sp. taxa were recognized here as alien because most of the specimens are hybrids of *P. pyraster* and *P. communis* (*Pyrus ×amphigenea*) (Dolatowski et al. 2004). Plant nomenclature follows Mirek et al. (2002). For this study the alien taxa were defined according to Danielewicz et al. (2020).

Scat collection and analysis

Scats of badgers *Meles meles*, foxes *Vulpes vulpes*, martens *Martes* spp. (*M. martes* and *M. foina*) and possibly also raccoon dogs *Nyctereutes procyonoides* were collected in 2009–2011 (N = 820) along nine parallel transects demarcated every 500–800 m. Each transect was about 4 km long and 2 m wide, crossing heterogeneous habitats and landscapes (opened and forested). According to home range areas of investigated carnivores (Zalewski et al. 2004; Kowalczyk et al. 2006) transects were designed to be as long as possible. In total, transects of 30.4 km were checked between days 10 and 20 of each month from June to November (5.6 km of the transects were excluded because they traversed wetland). Taking into account that a certain fraction of feces may pose difficulties in identification, especially based on their morphological features (Davison et al. 2002; Harrington et al. 2010; Morin et al. 2016), all scats were used only in joint analyses.

The collected samples were stored dry in paper envelopes, then searched for seeds with a binocular microscope and all seeds were counted and determined to species or genus at least (e.g. for *Rubus*, *Vitis*). Seed species were determined against our own reference seed collection and the seed atlas by Cappers et al. (2006). For the small seeds of *Vaccinium myrtillus*, which occurred in high numbers, the number of seeds was calculated from the weight of seeds found in the sample against the estimated weight of 1000 seeds.

Statistical analysis

The assemblage of fleshy-fruited plant species was represented by taxa that produce fruit containing numbers of seeds per fruit ranging from one in *Prunus* to more than 40 in *V. myrtillus* (Ehrlén and Eriksson 1993). *V. myrtillus*, producing small multi-seeded fruits, was excluded from some analyses based on seed quantity (seed load changes during vegetation period) because the large amount of its seeds consumed by carnivores biased the general share of other species that produce lower amounts of seeds per fruit. For qualitative analyses of seed frequency of occurrence (FO%, number of samples with i^{th} species as a share of all samples from a given carnivore), seeds of all plants were considered, including multi-seeded *V. myrtillus*.

A variable "fruiting period" (early, June–August; late, September–November) was used in computations for the dissimilarity of the taxonomic composition of dispersed seeds to reveal the main fruiting periods of plant species whose seeds were recorded in scats. The distinction of early and late fruiting periods is based on raw data exploration, which showed that most of the native plants bear fruit earlier in June–August and most of the alien plants bear fruit later in September–November (Figs 1, 2). For dissimilarity computations, non-metric multi-dimensional scaling (NMDS) was performed on a reduced data set; taxa with low frequency (i.e. those occurring in fewer than 10 samples; ~2% of scats containing seeds), were excluded from the analysis. That cut-off value was selected so as to reduce noise in the data but not to lose relevant information. We also ran NMDS on data sets extended with less frequent taxa (i.e. present in <10 samples), including the full data set. The obtained results (not shown in this paper) did not differ enough to change our conclusions. NMDS was based on Bray-Curtis distance and 9999 permutations. In this ordination, the closer the two points are, the more similar the corresponding samples with respect to the variables that went into making the

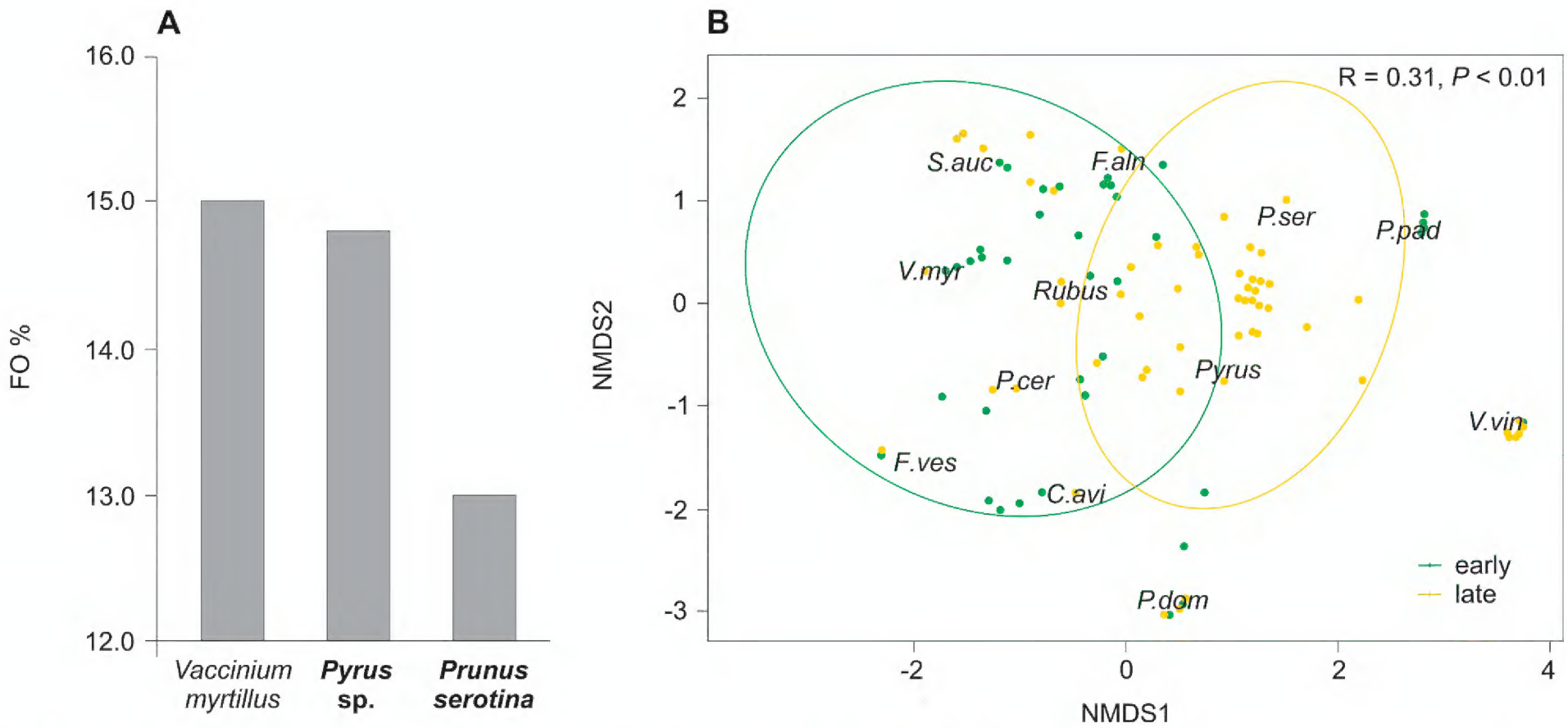

Figure 1. **A** seeds of the three most frequent plant species in carnivore scats (alien species in bold) **B** qualitative differentiation of seed assemblages from carnivore scats in relation to fruiting period, clearly separated into two assemblages of seeds of alien plants (late fruiting season) and native plants (early fruiting season). Stress = 0.002. Abbreviations of species: *C.avi* = *Cerasus avium*, *F.ves* = *Fragaria vesca*, *F.aln* = *Frangula alnus*, *P.cer* = *Prunus cerasifera*, *P.dom* = *Prunus domestica*, *P.pad* = *Prunus padus*, *P.ser* = *Prunus serotina*, *Pyrus* = *Pyrus* sp., *Rubus* = *Rubus* sp., *S.auc* = *Sorbus aucuparia*, *V.myr* = *Vaccinium myrtillus*, *V.vin* = *Vitis vinifera*.

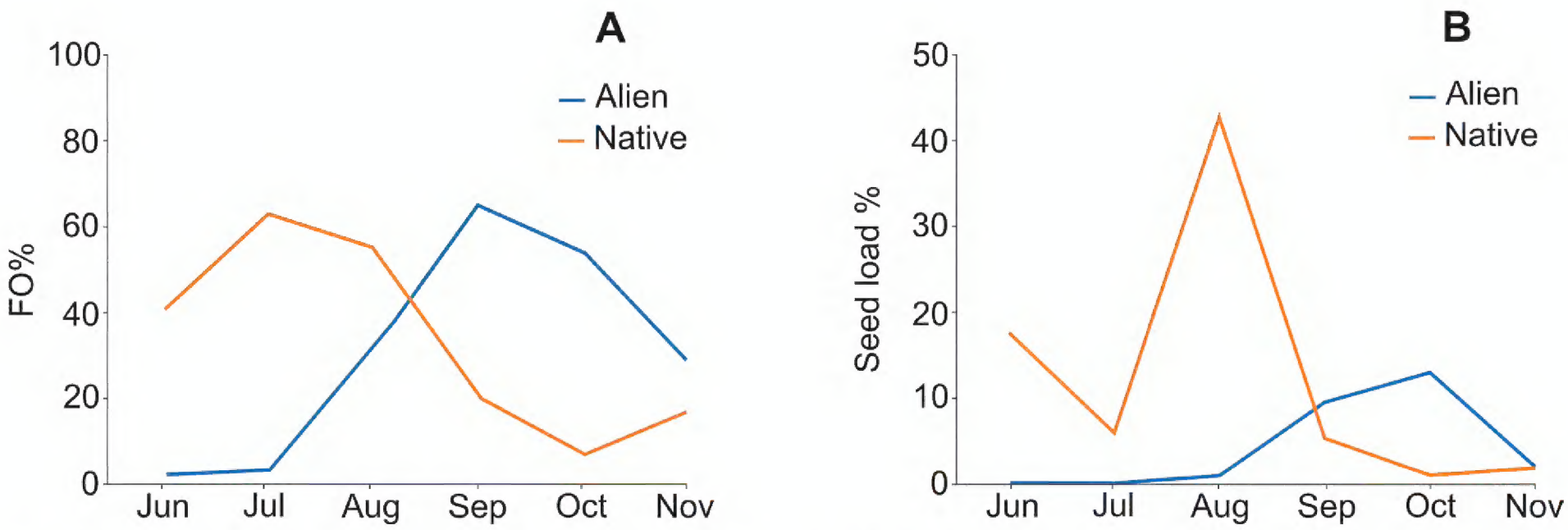

Figure 2. **A** distribution curves of frequency of occurrence (FO%) of seeds of alien and native plants, differing significantly during the fruiting period **B** the relationships between seed load of alien and native plants in scats with significant interactions (INT) between seed "status" (alien or native) and "month" of the vegetation period.

NMDS plot. In interpreting these results we used the 'anosim' statistic 'R' and significance level $P < 0.05$. An R value close to 1 suggests dissimilarity between groups, while an R value close to 0 suggests an even distribution of high and low ranks within and between groups (Clarke and Gorley 2001) – the higher the R value, the more dissimilar the groups are in terms of community composition. All multivariate analyses were conducted using 'metaMDS' and 'anosim' with the vegan package (Oksanen et al. 2022).

After backward selection of explanatory variables only two were chosen for further computations: "status" of seeds (alien or native, Tab. 1) and "month" (JUN–NOV) and the interactions between them as relevant results for interpretation of the dependent variable "seed load" (total number of seeds per scat sample). "Transect" and "year" were applied as random factors. A generalized linear mixed model (GLMM) was applied for all carnivores pooled together. Final results were computed with 'Anova' function using the car package (Fox and Weisberg 2019). Residuals versus expected values and overdispersion were verified using the DHARMa package (Hartig 2020). In case of significant deviations in residual diagnostics a negative binomial model was applied. We used the 'r.squaredGLMM' function to calculate marginal R^2_M (describes the proportion of variance explained by the fixed factors alone) and conditional R^2_C (describes the proportion of variance explained by both the fixed and random factors) (Nakagawa and Schielzeth 2013) of the MuMIn package (Bartoń 2019).

To test the significance of differences between the shares of feces with seeds of native and seeds of alien plant species during season, the data were analyzed with the Chi square test (χ^2). All statistical computations were performed with R v4.2.1 (R Core Team 2022).

Results

Seed assemblages in carnivore scats

In 2009–2011, 820 scats of four carnivore taxa were collected, 506 (61.7%) of which contained seeds (Table 1). The sampled feces contained seeds of 18 fleshy-fruited native and alien plant taxa. Most seeds represented species with multi-seeded fruits: *Vaccinium myrtillus* (94.6%), *Rubus* sp. (2.0%), and drupes

Table 1. Total number of seeds eaten by carnivorous mammals, recorded in feces, and descriptive statistics concerning seed load and seed FO%. * – data presenting the approximate number of seeds in the fruit according to Forest Service (1948), Ehrlén and Eriksson (1993), and Denisow (2006), ** – alien plant species according to Danielewicz et al. (2020).

	Plant species	Seeds per fruit*	N seeds in scats (N = 820)
Native species	*Vaccinium myrtillus*	25	314 675
	Rubus sp.	35	6 533
	Cerasus avium	1	1 189
	Fragaria vesca	47	3 216
	Prunus padus	1	476
	Ribes nigrum	28	1
	Sorbus aucuparia	3	313
	Convallaria majalis	4	170
	Frangula alnus	2	1 529
	Viscum album	1	44
	Sambucus nigra	3	17
	Sambucus racemosa	3	1
Alien species**	*Prunus domestica*	1	64
	Prunus cerasifera	1	136
	Prunus serotina	1	3 398
	Pyrus sp.	7	870
	Malus domestica	7	7
	Vitis sp.	3	161
Total			332 800
Total without *V. myrtillus*			18 126
Total alien seeds			4 636
Median of all seeds			16.0
Scats with alien seeds [%]			30.4
Scats with native seeds [%]			31.5

of *Prunus serotina* (1.0%) (Table 1). Five of the recorded species bear toxic fruits: *Convallaria majalis*, *Frangula alnus*, *Viscum album*, *Sambucus nigra* and *S. racemosa*. Six fleshy-fruited plant taxa whose seeds were recorded in carnivore scats were identified as alien in Central European forests (*Prunus serotina*, *P. cerasifera*, *Vitis* sp.), cultivars (*P. domestica*, *Malus domestica*) and hybrids (*Pyrus* sp.).

For all sampled scats, seeds of *Vaccinium myrtillus* (15.0%), *Pyrus* sp. (14.8%) and *Prunus serotina* (13.0%) were most frequent (FO%). Importantly, alien species occurred at high frequencies (Fig. 1A). Well pronounced and significant differences between the communities of dispersed seeds were found for the fruiting period ($R = 0.31$, $P < 0.01$, Fig. 1B). Seeds of alien plants were more abundant in September–November than in June–August, indicating the operation of two temporally independent frugivory patterns focused on native and alien fruit sources (Fig. 2).

Seed frequency – alien vs. native plants

In all sampled scats, seeds of alien and native plant species appeared at similar frequencies: respectively 30.4% (N = 249) and 31.5% (N = 258). In the late fruiting season (SEP–NOV), the frequency of all alien species in scats was higher than native ones: in September (65% vs. 20%), October (54% vs. 6%) and November

(28% vs. 16%, Fig. 2A). The reverse applied to the early fruiting season (JUN–AUG): in June (2% vs. 39%), July (3% vs. 63%) and August (30% vs. 55%, Fig. 2A). The frequency of occurrence of seeds in scats differed significantly between alien and native plant species; together the two seed frequencies form a double-peaked distribution through the course of the fruiting season (χ^2 = 231.9, df = 5, P < 0.01, Fig. 2A).

Seed load – alien vs. native plants

In total, 332 800 seeds of alien and native plants species were extracted from 820 scats (506 contained seeds), ranging in a single sample from 1 for drupes to even 27 500 seeds for multi-seeded fruits. For pooled data there was significant interaction between seed "status" (alien or native) and "month" (χ^2 = 29.2, df = 1, P < 0.001, R^2_M = 0.24, R^2_C = 0.35), and the seasonal changes of seed load for alien and native plants were also double-peaked, as in the case of frequency of occurrence (Fig. 2). The seed load of alien species in scats was higher than for native ones in September and October, reaching maximum values; in November, the values were equal (Fig. 2B). More than 95.7% (N = 4 436) of the seeds of alien plant species recorded in the carnivore scats were dispersed during the SEP–NOV period. The situation was the reverse for native plant species. Their seed content in carnivore scats was higher than for alien ones during the early fruiting period from June to August (Fig. 2B), as for FO%. Most of the native seeds (88.9%, N = 11 998) recorded in the sampled scats were dispersed during JUN–AUG, reaching maximum in August (Fig. 2B).

Discussion

Fruits are preferred by animals as an alternative food mainly as a source of sugars and lipids (Willson 1993). In many carnivores it is common to find an increase of fleshy fruit consumption and seed content in their feces over the course of the season (Kurek 2015), peaking in summer–early autumn (Goszczyński 1986; Martinoli et al. 2001; D'hondt et al. 2011) when they are most available. The general data on the amount of seeds in scats are somewhat similar in different regions of Europe (Herrera 1989; López-Bao and González-Varo 2011). In Central Europe the fruiting period begins in June with *Cerasus avium*, *Fragaria vesca* and *Vaccinium myrtillus*, and peaks in August–September when most native plant species produce fruits (Seneta et al. 2021). After that time the availability of fleshy fruits in the native flora declines, even though the vegetation season has not ended, while in this period there is a peak of fruiting of alien plant species. Our data revealed the coincidence of both factors – late fruiting of alien plants and the decreasing availability of native fruits during the vegetation period. Such a set of factors may promote the seed dispersal of alien plants by carnivores that produce fruits during this period (Bermejo and Guitian 2000; Wolkovich and Cleland 2011). In late summer and autumn, when fruits of native species are overripe or their supply is exhausted, fruits of *Pyrus* sp., *Prunus serotina* or other alien *Prunus* species become an important supplementary food. In such a phenological gap when native fleshy fruit is scarce, carnivores use alien plants as the only fruit sources. Limited availability of native fruits contributes to more efficient seed dispersal of alien plants

(Gosper et al. 2005; Heleno et al. 2013) and facilitates the spread of alien species (Gurvich et al. 2005).

Our data for seed frequency and seed load show clear differences in the seasonal pattern of frugivory in relation to native and alien fleshy-fruited plants. This constitutes evidence that the ripening phenology of alien taxa, different from that of native ones, may be beneficial for their seed dispersal when there is no alternative to their fruit. Late in the vegetation season, carnivorous mammals play a prominent role in dispersing numerous seeds of many alien plant species in European temperate forest ecosystems (López-Bao and González-Varo 2011). The high efficiency of alien seed dispersal by carnivores is confirmed by their high frequency and load recorded in scats.

The effects of the phenological patterns of fleshy fruit production in alien plants for seed dispersal are mostly recognized in birds (Gosper et al. 2005; Heleno et al. 2013; Vergara-Tabares et al. 2016, 2021), with very low attention being given to carnivorous mammals even though they are known to be seed dispersers of alien taxa (Fedriani et al. 2001; López-Bao and González-Varo 2011; Rost et al. 2012; Pereira et al. 2019). Most migrating frugivorous birds begin to abandon Central Europe in midsummer (Tomiałojć and Stawarczyk 2003), so the constant presence of carnivorous mammals in autumn may be crucial to the effective seed dispersal of late-fruiting alien plants, which may benefit directly from late ripening because autumn-fruiting species have higher removal rates than summer-fruiting species (Thompson and Willson 1979). In these circumstances the phenological gap seems to favor dispersal of the seeds of alien plants by carnivorous mammals having no other fruits to choose. The dispersal efficiency of alien seeds is here expressed in their high seed load and seed frequency in scats (Figs 1, 2). Following Gurvich et al.'s (2005) concept, we present our results as evidence that the later production and ripening of alien fruits during a period in which fruits of native plants are less available acts as a triggering attribute for seed dispersal of alien taxa. Carnivores then become seed dispersers of a wide spectrum of alien fleshy-fruited plants. Two crucial conditions of effective seed dispersal – non-destructive treatment of a seed in the mouth or gut, reflected in the low percentage of damaged seeds, and a high-quality deposition site where the seed may survive, germinate and become an adult (Shupp et al. 2010) – are fulfilled by carnivores. It has been shown that carnivores are not effective seed destroyers; most consumed seeds remain intact (Fedriani and Delibes 2009a). Herrera (1989) and also Pigozzi (1992) reported that less than 1% of seeds from carnivore feces may be damaged but that the percentage of intact seeds depends on the plant species. Visible proof of the second condition, the quality of the deposition site for alien plant seeds dispersed by carnivores, is seen in the characteristic clumps of their seedlings emerging from scats located mostly along linear elements of the landscape, such as road verges or road crossings (Suárez-Esteban et al. 2013), and concentrations of *P. serotina* and also cultivars of the genus *Prunus* and *Pyrus* sp. among badger setts and fox dens in forest habitats (Kurek et al. 2014).

Forest ecosystems are under strong pressure from invasive plant species, which pose serious problems for their protection (Waring and O'Hara 2005; Chabrerie et al. 2010). In conducting effective control of alien species, it is important to recognize their basic biology and ecology (Chmura and Sierka 2007; Woziwoda et al. 2018) with special attention to their dispersal strategies (Richardson et al. 2000). Our research focused on the commonest European carnivores showed that the

scale of fruit consumption and, as a result, seed dispersal of alien plant species in terms of their frequency and seed load in feces is relevant when compared to native ones. Based on the strength of these relationships expressed in the frequency and number of seeds of given plant species, it is possible to predict (Bradley et al. 2019) which plants pose or may pose a threat to forest ecosystems in the near future because it is often assumed that the impact of invasive plants is proportional to their population/diaspore density (Yokomizo et al. 2009; Elgersma and Ehrenfeld 2011; Panetta and Gooden 2017). It concerns large-fruited species especially, which are dispersed mainly by carnivorous mammals. The invasiveness forecast based on carnivores diet would be very useful especially when many attempts to predict which invading species are likely to become important weeds have largely been unsuccessful (Hobbs and Humphries 1995). According to phenological gap it is recognized that phenological differences between exotic and native species may contribute to the success of the invaders (Wolkovich and Cleland 2011). It means that the eradication plans should be fitted to phenology and biological and ecological traits of the alien species. Our results suggest that more attention should be paid to potentially more invasive late-fruiting species, being important fruit sources during the phenological gap, which in turn provides a more efficient dispersal for their seeds.

Conclusions

The decreasing availability of fruits of native plants before the end of the vegetation season in Central European temperate forests, creating a phenological gap, coincides with the late fruiting peak of alien plants. The temporal separation of fruiting periods favors alien plants and gives them a chance to achieve more efficient seed dispersal by carnivorous mammals, expressed in high seed frequency and seed load in their scats. Medium-sized carnivores, as seed dispersers of native and alien plants (Willson 1993; Fedriani and Delibes 2009a, 2009b; Murdoch et al. 2009; González-Varo et al. 2013; García-Rodríguez et al. 2021), cope with the changes in the fruiting pattern, showing an opportunistic feeding strategy that clearly responds to changes in food availability (Goszczyński 1986). During the phenological gap they simply switch from the decreasing supply of native fruits to more available late-fruiting alien species. The coincidence of two factors – the late fruiting period of alien plants and the decreasing availability of native fruits – promotes dispersal of alien plant seeds by carnivores in Central European forests.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Przemysław Kurek: Conceptualization, Methodology, Data sampling, Formal analysis, Writing – Original Draft, Writing – Rewiew & Editing, Visualization. Blanka Wiatrowska: Supervision, Methodology, Investigation, Writing – Original Draft. Łukasz Piechnik: Investigation, Resources, Editing. Jan Holeksa: Methodology, Supervision, Funding acquisition, Project administration.

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Data availability

All of the data that support the findings of this study are available in the main text.

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